Cenozoic Biogeographic History of the Eurythermal Genus *Retrotapes*, New Genus (Subfamily Tapetinae) from Southern South America and Antarctica

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ABSTRACT

Retrotapes, new genus, comprises a group of Neoaustral bivalves that appeared in the southern circumpolar regions by the Eocene and have since been confined to the high latitudes of the southern hemisphere. Its presence in the Tertiary strata of Antarctica and southern South America reflects an active faunal interchange between both regions during the Eocene. *Retrotapes* is here proposed to include to those Recent and Tertiary representatives of the Subfamily Tapetinae (Family Veneridae) from southern South America and Antarctica that had been previously placed in *Venus* Linné, 1758, *Marcia* H. and A. Adams, 1857, *Eurhomalea* Cossmann,1920, *Samarangia* Dall,1902, and *Kalelysia* Römer, 1857. The Argentine Tertiary species *Retrotapes ninfasiensis*, new species, *R. fuegoensis*, new species, *R. striatolamellata* (Ihering, 1897) and *R. scutata* (Ihering, 1907) are here described and illustrated. The Recent Argentine *Venus exalbida* Chemnitz, 1795 and *Venus lenticularis* Sowerby, 1835, the Antarctic *V. antaretica* Sharman and Newton, 1894 and *V. newtoni* Wilckens, 1911 (Eocene-early Oligocene?, La Meseta Formation), and the Neogene Chilean species *V. navidadis* Philippi, 1887 and *V. colchaguensis* Philippi, 1887 are also included in this new genus.

Key words: Tapetinae, *Retrotapes*, new genus, biogeography, Neoaustral, Tertiary, Argentina, Chile, Antarctica.

INTRODUCTION

The Subfamily Tapetinae (Family Veneridae) shows a moderately high degree of endemism in Recent as well as in Tertiary faunas. The known geographic distribution of most living tapetines is mainly restricted to the southern hemisphere. This subfamily is particularly abundant in the southern Indo-Pacific region, where it is represented by more than seventy species. Most of the Indo-Pacific genera, among them *Katelysia* Römer, 1857, *Marcia* H. & A. Adams, 1857, *Granicorium* Hedley, 1906, *Hemitapes* Römer, 1864, *Notirus* Finlay, 1928, *Notopaphia* Oliver, 1923, *Eumarcia* Iredale, 1924, *Paphirus* Finlay, 1927, and *Gomphinella* Marwick, 1927, are restricted to New Zealand and Australia. Others, including *Gomphina* Mörch, 1853, *Venerupsis* Lamarck, 1818, *Ruditapes* Chiamenti, 1900, *Tapes* Mergele von Mühlfeld, 1811, and *Paphia* Röding, 1798, are also found beyond those regions.

In contrast, Recent tapetines are poorly represented in the littoral zones along both coasts of the American continents. The subfamily is known from only twelve living North American species distributed among the genera *Ruditapes*, *Liocyma* Dall, 1870, *Psephidia* Dall, 1902 and *Irus* Schmidt, 1818, as well as five South American taxa assigned to the genera *Eurhomalea* Cossmann, 1920 and *Retrotapes*, new genus.

The fossil record in the Americas reveals that Tapetinae were more abundant in the Tertiary than in the Recent fauna. Two diverse and different assemblages appeared during the Tertiary, one restricted to North America, the another to austral latitudes. The northern assemblage comprises the endemic genera *Liocyma*, *Cyclorisma* Dall, 1902, *Psephidia* and *Sinonia* Stephenson, 1952, as well as taxa with european affinities such as *Mercimonia* Dall, 1902, *Flaventia* Jukes-Browne, 1908, *Paraesa* Casey, 1952 , *Legumen* Conrad, 1858 and *Textivenus* Cossmann, 1886. The less diverse austral assemblage, characterized by *Eumarcia*, *Katelysia*, *Atamarcia* Marwick, 1927 and *Retrotapes*, appeared during the early Tertiary in the southernmost region of South America and Antarctica.

Figure 1. Stratigraphic distribution of *Retrotapes*, new genus, in South America and Antarctica.

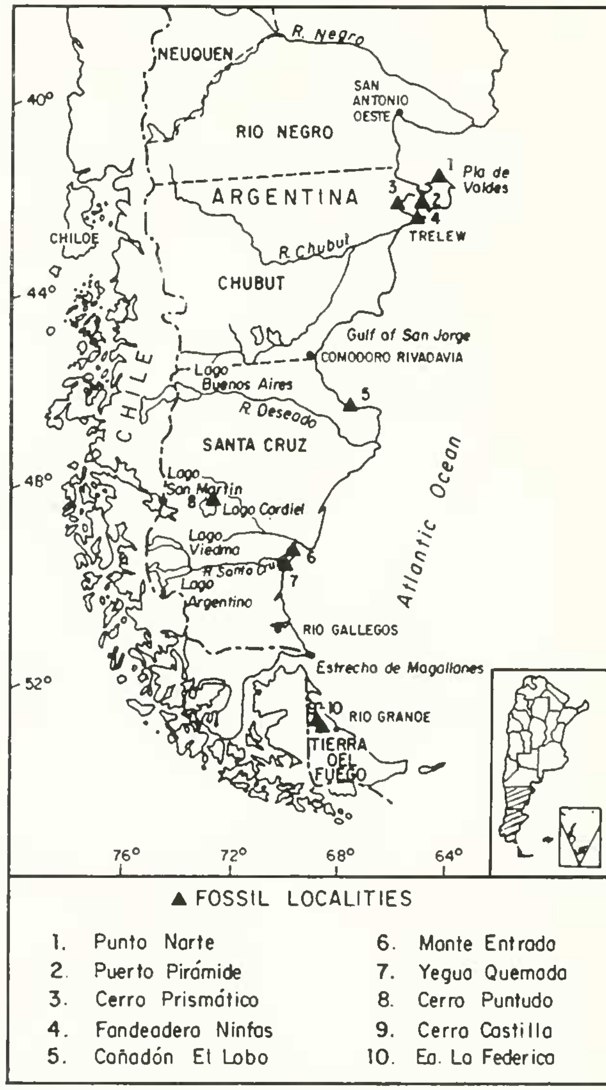


Figure 2. Geographic distribution of fossil localities referred to in this paper.

The species that are here included in *Retrotapes* occur in the Tertiary rocks of Chile, Antarctica and Argentina, and are at present distributed in the littoral zones along both coasts of South America (Figure 1), where they are represented by *R. lenticularis* (Sowerby, 1835) and *R. exalbida* (Chemnitz, 1795).

This paper includes the systematic description of the Tertiary Argentine representatives of *Retrotapes: R. ninfasiensis* new species (Puerto Madryn Formation, middle Miocene), *R. fuegoensis* new species (Carmen Silva Formation, late Oligocene-early Miocene), *R. striatolamellata* (Ihering, 1897) (Monte Léon Formation, late Oligocene-early Miocene) and El Chacay Formation (late Eocene) and *R. scutata* (Ihering, 1907) (San Julián Formation, late Eocene). *Venus antarctica* Sharman and Newton, 1894 and *V. newtoni* Wilckens, 1911 from the Eocene-early Oligocene? La Meseta Formation (Antarctica), and the Chilean species *V. navidadis* Philippi, 1887 (early Miocene), *V. colchaguensis* Philippi, 1887 (early Miocene-Pliocene) and *V. lenticularis* (Pliocene-Holocene), along with the Recent *V. exalbida*, are also placed in *Retrotapes*.

MATERIAL AND METHODS

The fossil material reported here came from the thick, marine, sedimentary, Tertiary sequence exposed along the eastern coast of Patagonia from San Antonio Oeste (Río Negro Province), southward to Isla Grande of Tierra del Fuego, and at Cerro Puntudo (Lago Cardiel), a locality situated in the western region of Patagonia (Santa Cruz Province) (Figure 2). Lithostratigraphic units yielding representatives of *Retrotapes* are the Puerto Madryn Formation (Haller, 1978), the Monte León Formation (Bertels, 1970), the Carmen Silva Formation (Codignotto & Malumián, 1981), the San Julián Formation (Bertels,

1970) and the El Chacay Formation (Chiesa & Camacho, 1984).

The Puerto Madryn Formation, exposed at Peninsula Valdés (Chubut Province), is believed to represent one of the youngest Tertiary marine units recognized in Patagonia, having been reported by del Río (1988, 1992) as being of middle Miocene age. This formation consists of 150 meter thick, whitish cinerites and yellowish sandstones alternating with highly fossiliferous calcareous sandstones and muddy or sandy shelly beds. *Retrotapes* is abundant at the basal ochreous shelly sandstones that are exposed at Cerro Prismático (horizon N 2, del Río, 1992), where it is associated with "*Chlamys*" *actinodes* (Sowerby, 1846), *Purpurocardia leonensis* del Río,1986, *Glycymerita magna* del Río, 1992, *Aequipecten paranensis* (d'Orbigny, 1842), *Dosinia meridionalis* (Ihering, 1897) as well as with the gastropod *Valdesia valdesiensis* del Río, 1985. *Retrotapes* is less common in the gray, massive, fine sandstones that comprise the base of the section at Punta Norte (horizon PN 2, del Río, 1992), where articulated specimens have been found in life positions along with *Anadara (Rasia) lirata* (Philippi, 1893), *Glycymeris longioriformis* del Río, 1992, *Lucinisa* sp., "*Cyclocardia*" *nortensis* del Río, 1986, *Dosinia meridionalis* (Ihering, 1897), *Dosinia cuspidata* del Río, 1994, *Ameghinomya meridionalis* (Sowerby, 1846) and *A. argentina* (Ihering, 1897). *Retrotapes* also occurs in the strata placed at the top of the sequence exposed at Punta Ninfas (horizon F 9, del Río, 1992) and is associated with *Glycymerita magna* del Río, 1992, *Amusium paris* del Río, 1992, and *Aequipecten paranensis* (d'Orbigny, 1842).

Retrotapes has also been collected from exposures of the late Oligocene Monte León Formation that crop out at the mouth of the Santa Cruz River (Santa Cruz Province). Here it is locally abundant in the highly fossiliferous, coquinoid sandstones situated 80 meters above sea level at Monte Entrada and in the sandy lenses present at the sea cliffs at Las Cuevas. Fossil material is well preserved at both localities where disarticulated valves are associated with a rich bivalve fauna characterized by *Cucullaea alta* (Sowerby, 1846), *Neilo ornata* (Sowerby, 1846), *Pecten proximus* Ihering, 1897, *Venericardia inaequalis* Philippi, 1887, *Limopsis insolita* Sowerby, 1846, *Australocallista iheringii* (Cossmann,1898), *Dosinia meridionalis* Ihering, 1897, *Perna quadrisulcata* Ihering, 1897 and *Phacoides crucialis* Ihering,1907.

Specimens of *Retrotapes* found at the Carmen Silva Formation (late Oligocene-early Miocene) occur in pebbly shelly sandstones at the top of the sequence that crops out at Cerro Castillo and Estancia La Federica. Material is abundant and well preserved, with most of the specimens consisting of articulated valves.

Material coming from the San Julián Formation was collected by C. Ameghino from sedimentary marine outcrops at Cañadón El Lobo (= Cañadón Tournöuer), close to Punta Casamayor. The age of the San Julián Formation is still debated, ranging from late Eocene to early Oligocene (Nañez, 1988; Camacho, 1984, 1995), as recently documented by del Río (1995). Only one fairly well-preserved valve of *Retrotapes* is known from the uppermost, highly-fossiliferous, orange coquinoid sandstones that alternate with green or yellowish gray silstones and sandstones exposed at Cañadón El Lobo.

Retrotapes is poorly represented in the El Chacay Formation, exposed at Cerro Puntudo (Lago Cardiel). Chiesa and Camacho (1994) placed this unit in the late Eocene based on biostratigraphic correlations with the San Julián Formation.

Specimens described in this paper are housed in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina, in the Centro de Investigaciones en Recursos Geológicos (CIRGEO-PI), Buenos Aires, Argentina, Facultad de Ciencias Exactas y Naturales of the Universidad de Buenos Aires (CPBA), Buenos Aires, Argentina, Dirección Nacional Servicio Geológico (DNSG), Buenos Aires, Argentina and in the Department of Earth and Atmospheric Science, Purdue University (PU), Indiana, USA.

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Linné, 1758
Class BIVALVIA Linné, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. & A. Adams, 1856
Superfamily VENEROIDEA Rafinesque, 1815
Family VENERIDAE Rafinesque, 1815
Subfamily TAPETINAE H. & A. Adams, 1857

Diagnosis: Members of this subfamily are characterized by having smooth inner ventral margins and three cardinal teeth in each valve, with at least two of them grooved or bifid. Most Tapetinae have exterior surfaces with commarginal lines and/or grooves, while others have polished surfaces or very fine radial threads. Though no attention has been paid to the presence of a lunule or the arrangement of cardinal teeth, these characters, along with the general outline of the cardinal platform, are of taxonomic importance at the generic level. When present, and viewed dorsally, the lunule may be concave or convex, and is limited by a groove and/or ridge that is distinguished from the remaining surface of the shell by its different ornamentation, or by the presence of a groove.

Hinge characters have proven to be the most useful morphological feature for distinguishing among genera. Cardinal teeth may be placed on a thin, slender, cardinal platform with a straight ventral margin, or situated on a short, broad, strongly arcuate platform. While some genera are characterized by having teeth that diverge from a point situated below the beaks, others have non-divergent teeth (Figure 3). Divergent teeth are characterized by a strongly forward-inclined anterior tooth, a vertical median tooth, and a backward-inclined posterior tooth. Genera with non-divergent teeth may have three cardinal teeth sloping backwards (posterior tooth nearly

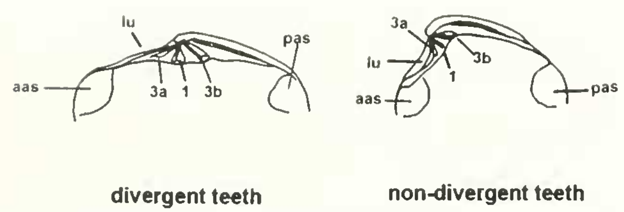


Figure 3. Hinge teeth types in Tapetinae. aas, anterior adductor muscle scar; lu, lunule; pas, posterior adductor muscle scar; 1,3a,3b, cardinal teeth.

horizontal) or have the median and posterior teeth inclining backwards, with the anterior tooth being vertical.

Genus *Retrotapes*, new genus

Patagomalea del Río, 1991:93, nomen nudum.

Diagnosis: Shell large to medium sized, highly variable in outline. Escutcheon facing opposite valve, usually wider, smoother on left valve than on right in adults. Lunule large to medium sized, deeply impressed, strongly differentiated from remaining shell surface, highly to moderately concave, nearly vertical, with longitudinal median sulcus, bounded by deep lunular groove. Hinge heavy, short, arcuate behind teeth, with three long cardinal teeth. Right and left posterior teeth nearly horizontal in some species, left and right anterior teeth nearly vertical to strongly sloping backwards, nearly paralell to posterior teeth; left median tooth, right median and posterior teeth bifid or grooved.

Type species: *Retrotapes ninfasiensis*, new species.

Type locality: Valdés Peninsula, Chubut Province, Argentina, Puerto Madryn Formation (Middle Miocene).

Stratigraphic range: Eocene to Holocene, southern South America and Antarctica.

Etymology: *retro-* L. backwards. Referring to the inclination of non-divergent cardinal teeth towards the posterior region of the shell.

Remarks: Recent as well as fossil species belonging to *Retrotapes* have previously been placed in *Venus* Linné, 1758, (Philippi, 1887; Ihering, 1897), in *Marcia* (Dall, 1902; Ihering, 1907; Riveros & Gonzalez, 1950), in *Samarangia* Dall, 1902 (Jukes-Browne, 1908; Carcelles, 1944; Carcelles & Williamson, 1951; Castellanos, 1970; Rios, 1975) in *Eurhomalea* (Keen, 1954; Soot-Ryen, 1959; Ramorino, 1968; Fisher-Piette & Vukadinovic, 1977; Malumián *et al.* 1978, Zinsmeister, 1984; Stilwell & Zinsmeister, 1992) and in *Katelysia* (Dall, 1902; Jukes-Browne, 1908; Riveros & Gonzalez, 1950).

The taxonomic placement of the Holocene South American species *Venus exalbida* (Figures 22–23, 41) and *Venus lenticularis* (Figures 19–21), here assigned to *Retrotapes*, has long been debated, and the phylogenetical relationships of these species within the family Veneridae were misunderstood. Dall (1902) incorrectly interpreted Fischer's (1887) statement about *V. exalbida* being the type species of the genus *Marcia*, considered *Samarangia* (type species *Venus quadrangularis* Adams & Reeve, 1850) to be a section of *Marcia*, and placed *V. lenticularis* in *Samarangia*. He thought *V. exalbida*, *V. lenticularis* and *V. quadrangularis* to be part of a closely related group of species related to *Marcia*. Jukes-Browne

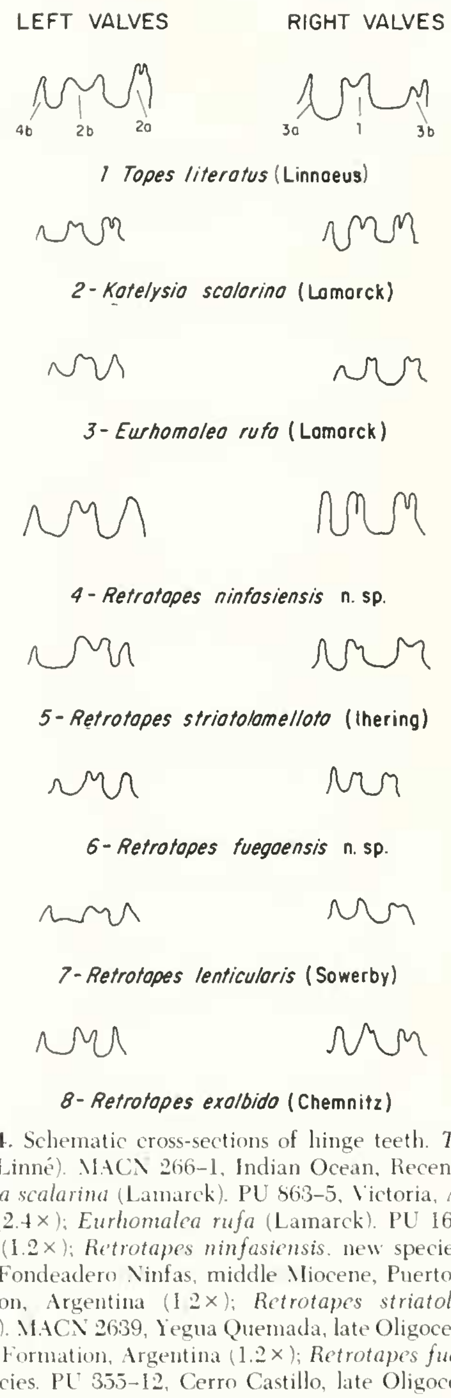
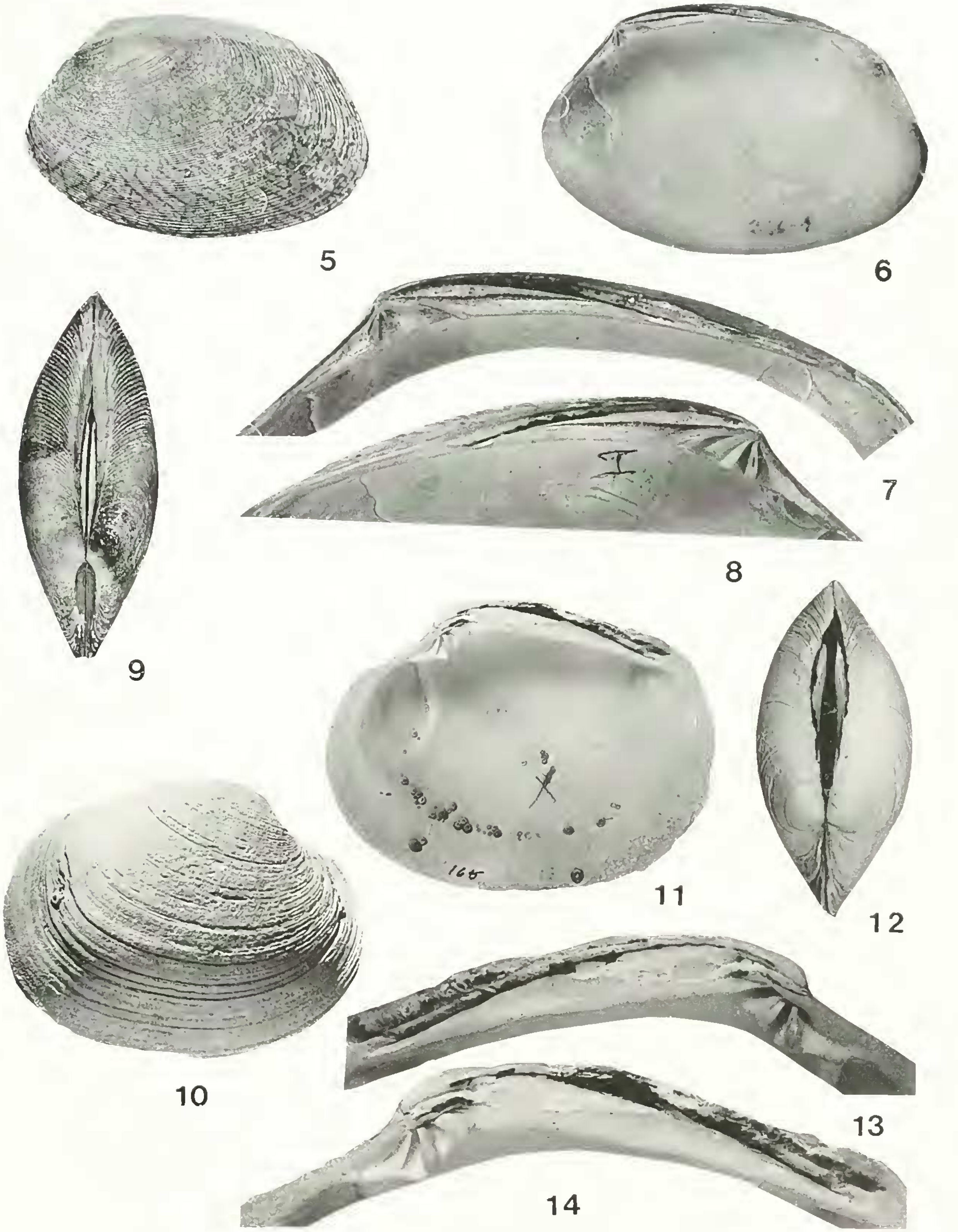


Figure 4. Schematic cross-sections of hinge teeth. *Tapes literatus* (Linné). MACN 266-1, Indian Ocean, Recent (2.4×); *Katelysia scalarina* (Lamarck). PU 863-5, Victoria, Australia. Recent (2.4×); *Eurhomalea rufa* (Lamarck). PU 165, Chile, Recent. (1.2×); *Retrotapes ninfasiensis*. new species. CPBA 15.110, Fondeadero Ninfas, middle Miocene, Puerto Madryn Formation, Argentina (1.2×); *Retrotapes striatolamellata* (Ihering). MACN 2639, Yegua Quemada, late Oligocene, Monte León Formation, Argentina (1.2×); *Retrotapes fuegoensis*, new species. PU 355-12, Cerro Castillo, late Oligocene-early Miocene, Carmen Silva Formation, Argentina (1.2×); *Retrotapes lenticularis* (Sowerby). PU 165, Chile, Recent (1.2×); *Retrotapes exalbida* (Chemnitz) MACN 21.172, Argentina, Recent (1.2×).



Figures 5–9. *Tapes literatus* (Linné). MACN 266-1, Indian Ocean, Recent. **5.** Exterior view of left valve (1×). **6.** Interior view of right valve (1×). Enlargements of **7.** right and **8.** left hinges (2×). **9.** Dorsal view of an articulated specimen (1×). **Figures 10–14.** *Eurhomalea rufa* (Lamarck). PU 165, Chile, Recent. **10.** Exterior and **11.** interior views of right valve (1×). **12.** Dorsal view of an articulated specimen (1×). Enlargement of **13.** left and **14.** right hinges (2×).

(1908) designated *Venus pinguis* Chemnitz, 1782 (= *V. opima* Gmelin, 1791) as the type species of *Marcia*, and excluded *V. exalbida* from this genus.

Venus quadrangularis (see Fischer-Piette & Vukadinovic, 1977:22, figs.207–211, for illustrations of the species) cannot be related to either *V. exalbida* or *V. lenticularis* because of the presence in *V. quadrangularis* of a smooth exterior surface, a pustular left anterior lateral tooth and an entire pallial line, characters that allowed Keen (1969) to segregate *Samarangia* in the Subfamily Samarangiinae. Other diagnostic features, including the hinge and lunular characteristics of *V. exalbida*, *V. lenticularis*, as well as those of their Tertiary ancestors, require the erection of the new genus *Retrotapes*. It is placed in the Subfamily Tapetinae on the basis of the presence of shells with a smooth inner ventral margin, moderate to very deep pallial sinus, three cardinal teeth in each valve with two of them deeply grooved or bifid, and the absense of lateral teeth. Morphological features that distinguish *Retrotapes* from the remaining genera of the subfamily are the presence of non-divergent cardinal teeth and a well defined, concave lunule, bounded by a deep lunular groove and ridge.

Eurhomalea, represented by its type species *E. rufa* (Lamarck, 1818) (Figures 4, 10–14) and by *E. salinensis* Ramorino, 1968 (see Ramorino, 1968:218, pl.3, fig.2, pl.9, figs.2–3 for illustrations of the type species), is distributed along the Peruvian and Chilean coasts and has recently been placed in the Subfamily Chioninae (Fischer-Piette & Vukadinovic, 1977). However, the presence of a smooth inner ventral margin in *Eurhomalea* indicates that it is more accurately assigned to the Subfamily Tapetinae. It clearly differs from *Retrotapes* in lacking both lunule and escutcheon, in having a straight dorsal margin, a more antero-posteriorly elongate shell, and a narrower hinge plate than *Retrotapes*. Moreover, the cardinal teeth are markedly smaller than those of *Retrotapes* and quite divergent from a point situated below the beaks. The anterior cardinal teeth of both valves in *Eurhomalea* slope forward. The left posterior and right anterior cardinal teeth are much lower than in *Retrotapes*, and the left middle, and right posterior and middle teeth are only shallowly grooved.

Katelysia (type species: *Venus scalarina* Lamarck, 1818) (Figures 4, 25–28), a middle Miocene-Holocene genus confined to New Zealand and Australia, differs in having a different outline, a narrower lunule and escutcheon, a shallower pallial sinus, and a shorter cardinal teeth than *Retrotapes*.

Marcia opima, the Indo-Pacific type species of *Marcia*, was illustrated by Abbott and Dance (1986:363). The genus differs from *Retrotapes* in having a smooth exterior shell surface, a high umbonal area, a weakly defined escutcheon, and a nearly smooth and lightly impressed lunule that lacks a lunular groove. These genera may also be separated because *Marcia* has lower, narrower and more widely divergent teeth than *Retrotapes* with the anterior cardinal teeth inclining forward.

Eumarcia (type species *Venus fumigata* Sowerby, 1853, illustrated by Lamprell & Whitehead, 1992, pl.74, fig.589; Abbott & Dance, 1986:363) a common genus in New Zealand and Australia, is easily separated from *Retrotapes* on the basis of its oval and smooth shells, a lunule that is not impressed and that is bounded by a weak line, divergent teeth with left anterior and middle cardinal teeth deeply grooved and equal in size, and in having a left posterior tooth that is fused to nymph.

The Tertiary New Zealand *Atamarcia* (type species *Eumarcia sulcifera* Marwick, 1927, figs.200, 203, 205, early Oligocene-late Pliocene) differs from *Retrotapes* in being sculptured with commarginal grooves, in having a fairly impressed lunule, with a shallow lunular groove, divergent teeth with curved posterior teeth, and with the left anterior and middle teeth being of equal width.

The monotypic, lower Pliocene *Opimarcia* Marwick, 1948, (type species: *O. healyi* Marwick, 1948, pl.5, figs.1, 2, 4) is distinguished from *Retrotapes* in having oval, inflated shells, very prominent beaks, a poorly defined lunule not bounded by a lunular groove, a fairly well-developed escutcheon, fine irregular commarginal ridges on the posterior and anterior ends of valves, a shorter pallial sinus than *Retrotapes*, and divergent teeth with a strongly curved right posterior tooth and a triangular, deeply grooved left anterior tooth.

Tapes (type species: *Venus literatus* Linné, 1758) (Figures 4–9) has shells that are more antero-posteriorly elongated than those of *Retrotapes*, and have a straight, horizontal dorsal margin, acuminate anterior margin, a rounded pallial sinus, straight or slightly arcuate hinge margin and a grooved left anterior cardinal tooth.

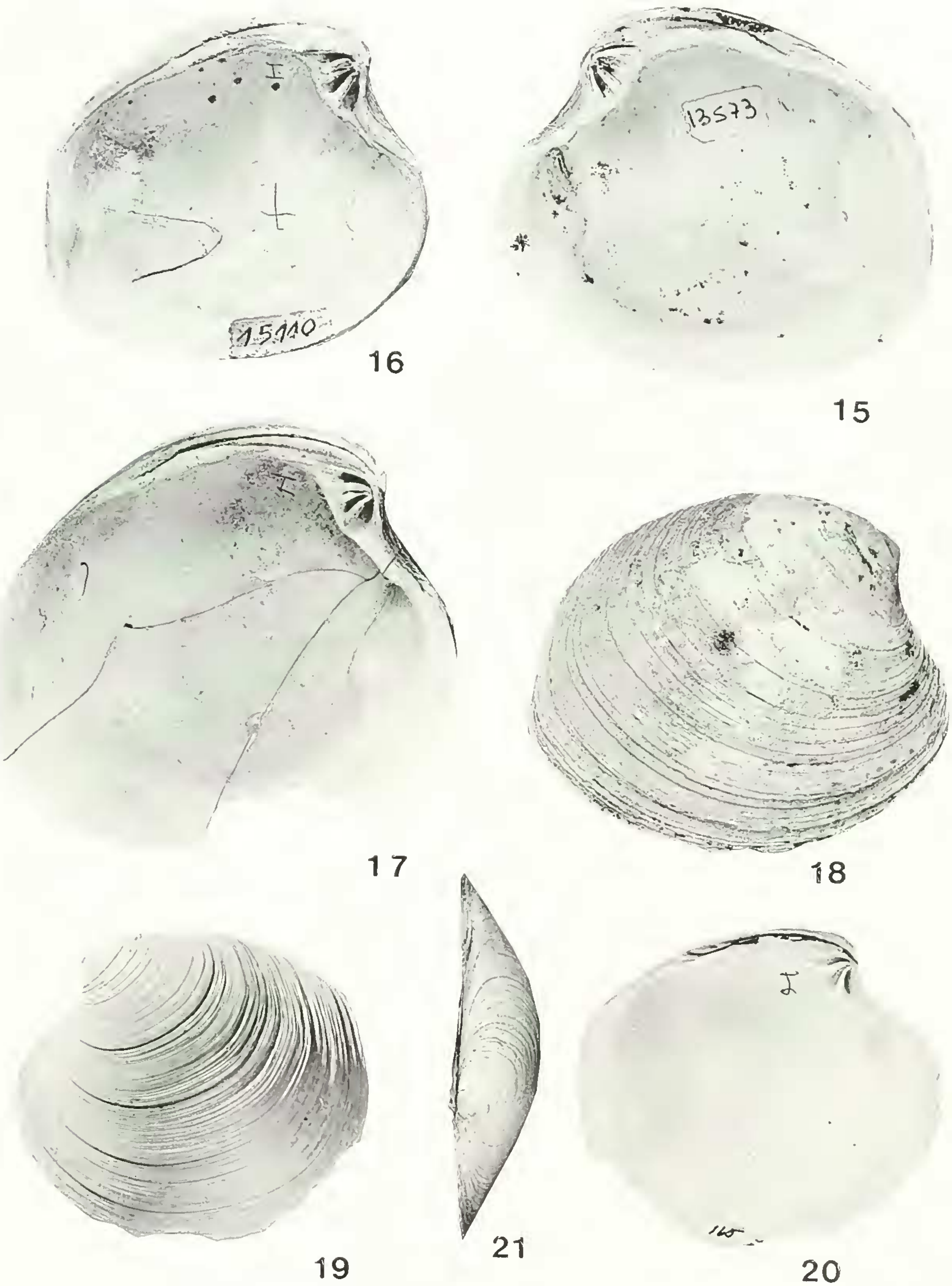
The oldest presently known record of *Retrotapes* dates to the late Eocene. This genus occurs in the San Julián Formation and the El Chacay Formation (Argentina), where is represented by *R. scutata* and *R. striatolamellata*, and in the lower and middle sections of the La Meseta Formation (late Eocene-Oligocene?, Antarctica) where *R. antarctica* and *R. newtoni* have been found.

Retrotapes ninfasiensis, new species
Figures 15–18, 40

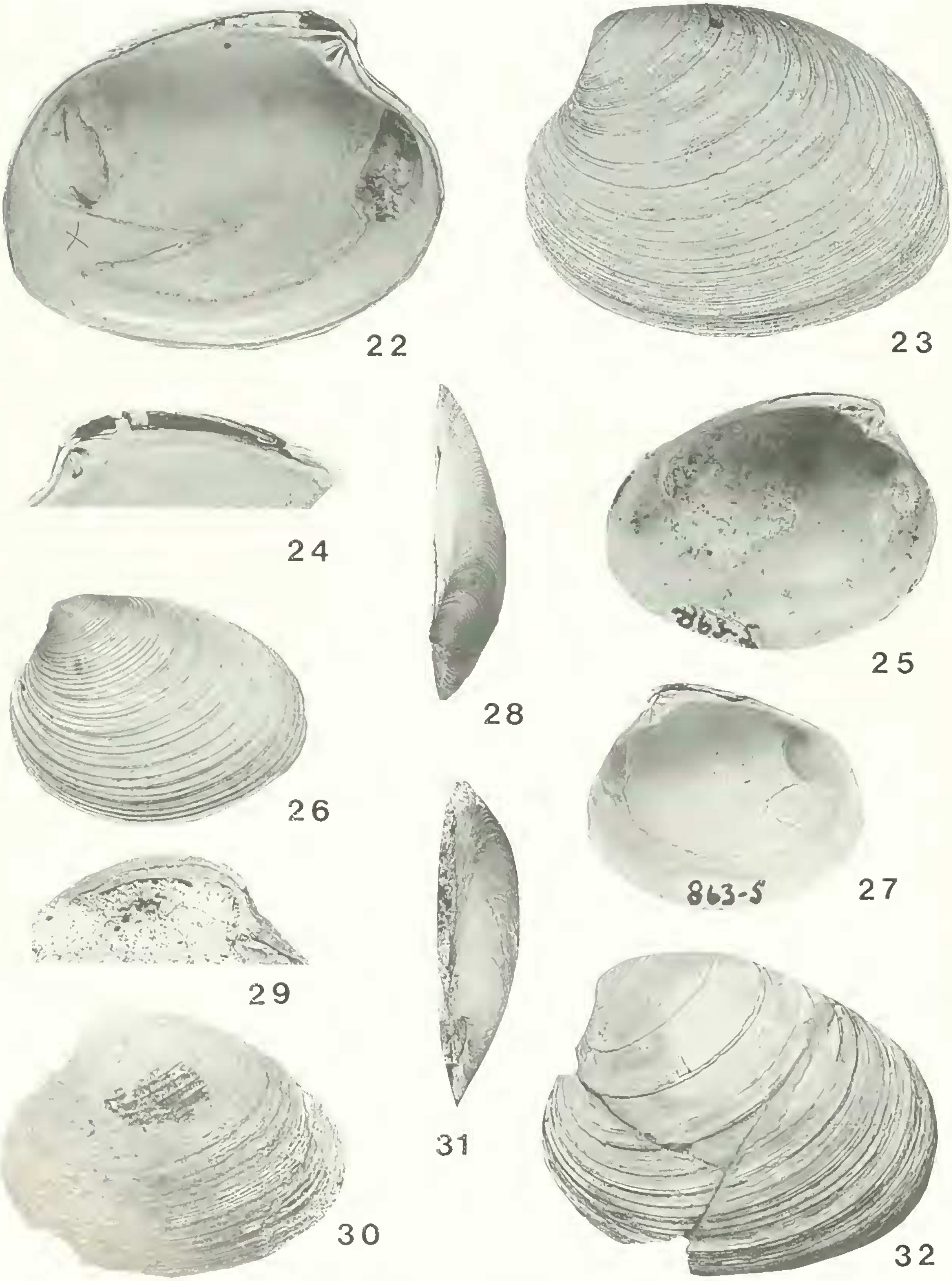
Marcia striatolamellata Frenguelli, 1926, not *M. striatolamellata* Ihering, 1897.

Diagnosis: Shell thick, ovate to subrectangular. Lunule deeply concave, nearly vertical, strongly inclined toward opposite valve. Cardinal teeth straight, high, long, thick. Median and anterior teeth sloping backwards, posterior cardinal teeth horizontal. Pallial sinus triangular, moderately short.

Description: Shell thick, large, ovate to subrectangular, weakly convex, ranging from longer than high to nearly equidimensional. Umbones small, at anterior quarter of length. Dorsal margin moderately to strongly convex, posterior margin truncated to weakly convex, ventral margin nearly straight to weakly convex, anterior margin convex. Lunule concave, with longitudinal median lunular groove, nearly vertical, strongly inclined toward opposite valve, bounded by deep groove and well marked



Figures 15–18. *Retrotapes ninfasiensis*, new species Puerto Madryn Formation, middle Miocene. **15.** Interior and **18.** exterior views of right valve of holotype, CPBA 13.573. Cerro Prismático. **16.** Interior view of left valve of paratype, CPBA 15.110, Fondeadero Ninfas. **17.** Interior view of left valve of paratype, CPBA 15.090, Punta Norte **Figures 19–21.** *Retrotapes lenticularis* (Sowerby), PU 165. Chile, Recent. **19.** Exterior, **20.** interior and **21.** dorsal views of left valve. All figures 1×



Figures 22–24. *Retrotapes exalbida* (Chemnitz) MACN 21 172, San Matías Gulf, Argentina, Recent. All figures 1×. **22.** Interior and **23.** exterior views of left valve. **24.** View of right hinge. **Figures 25–28.** *Katelysia scalarina* (Lamarck), PU 865-5, Victoria, Australia, Recent. All figures 2×. **25.** Interior, **26.** exterior, and **28.** dorsal views of left valve. **27.** Interior view of right valve.

ridge. Escutcheon on left valve wide, long, inclining toward right valve and only slightly sculptured with fine commarginal ridges; escutcheon on right valve poorly differentiated and ornamentated as remaining shell surface. Hinge short, narrow, strongly arcuate behind teeth, with three high, thick cardinal teeth per valve (Figure 4). Anterior and median teeth strongly inclined backwards, posterior teeth nearly horizontal. Right valve with deeply grooved posterior tooth separated from nymph by socket, followed by ridge, median cardinal bifid with lamellar posterior section, anterior tooth thick, equal in height to median tooth; socket for left median tooth with radial lamella. Left hinge with strong, smooth, anterior tooth, median tooth deeply grooved, with both parts equal in size, lower than anterior tooth. Posterior tooth lamellar, slightly arched, with superimposed ridge on posterior face, separated from nymph by shallow groove. Anterior adductor muscle scar oval, more deeply impressed, larger than posterior muscle scar; anterior pedal retractor muscle scar small, deeply excavated, placed above adductor. Pallial sinus relatively short, triangular, with horizontal dorsal margin, straight, ascending ventral margin; apex pointed. Exterior ornamented with widely-spaced, thin, lamellar commarginal ridges, much more numerous near ventral margin; interspaces sculptured with very fine radial threads.

Material examined: Holotype, CPBA 13.573, right valve, Cerro Primático, height 66.6 mm, length 76.2 mm. Paratypes, CPBA 15.090, left valve, Punta Norte, height 77.1 mm, length 81.9 mm, CPBA 15.110, left valve, Fondeadero Ninfas height: 60,0 mm, length: 66,0 mm; 19 left valves, 16 right valves, one articulated specimen, Punta Norte (PN 2): CPBA 15.087–15.089, CPBA 13.287-13.288, Fondeadero Ninfas (F 9): CPBA 12.345, CPBA 15.1 1 0, Cerro Prismático (N 2): CPBA 12.501, CPBA 11.646–11.650, CPBA 12.343, CPBA 12.502, CPBA 13.572, 13.574–13.575 (del Río collection)

Stratigraphic and geographic distribution: Puerto Madryn Formation, middle Miocene. Valdés Peninsula, Chubut Province.

Remarks: Specimens of *Retrotapes ninfasiensis* have erroneously been attributed to *Marcia striatolamellata* (Frenguelli, 1926), a closely related, late Oligocene species that occurs in the Monte León Formation of Santa Cruz Province. *Retrotapes striatolamellata* (Figures 33, 37–39, 42–47) may be differentiated by its longer, more convex shells, straighter dorsal margin, a lunule that is more concave and not inclined toward the opposite valve, less prominent teeth, a left anterior cardinal tooth that is less inclined backwards, being slightly arched forwards in most specimens and higher or equal in height than the median cardinal (Figure 4), and a pallial sinus that is tongue-like and longer than in *R. ninfasiensis*. *Retrotapes antarctica* (Sharman & Newton,1894, fig.3), from the La Meseta Formation (Antarctica, Eocene- early Oligocene?), differs in having a trigonally suboval outline with the dorsal margin strongly sloping backwards and rounding to the posterior margin, by the presence of a shallowly concave, narrower lunule not inclined toward the opposite valve, and a narrower, shorter pallial sinus than *R. ninfasiensis*. Moreover, *R. antarctica* has narrower teeth than *R. ninfasiensis*, the right anterior tooth inclines forwards, the left anterior tooth is grooved and higher than the median one, and the left median tooth is deeply grooved, with both sections equal in width. *Retrotapes ninfasiensis* is easily separated from *R. navidadis* (Philippi, 1887, pl.14, fig.4, Navidad Formation) because the Chilean Miocene species has a thinner and smaller shell with an acuminate anterior margin, straighter dorsal margin, more prominent beaks and a narrower lunule that is not inclined to the opposite valve. Cardinal teeth of *R. navidadis* are narrower and much shorter than in *R. ninfasiensis*, the right anterior cardinal tooth is vertical, but its anterior face inclines forward, while the left anterior cardinal tooth is lightly curved and also slopes forward. *Retrotapes lenticularis* (Sowerby) (Riveros & Gonzalez, 1950:fig.30) (Figure 19–21), a species distributed along the Chilean litoral from Coquimbo to Valparaiso, and also present in the Pleistocene outcrops in Central Chile (Herm, 1969:pl.13, figs.1–4), has subcircular shells with straight to lightly convex dorsal margins, smaller lunules not inclined toward the opposite valve, and much narrower and shallower grooved cardinal teeth than *R. ninfasiensis*. The right posterior cardinal tooth inclines backwards and is separated from the nymph by a groove, the right anterior tooth varies from being vertical to slightly inclined forward, and the left anterior and median teeth are curved. The exterior surface is covered by fine commarginal ridges, widely spaced, deep commarginal grooves, and very fine radial threads.

The Recent *R. exalbida* (Castellanos, 1970:250, pl.22, figs.4–5) (Figures 22–24, 41) is characterized by subrectangular and more inflated shells, with a shallower lunule, lower and shorter cardinal teeth with a deeper, grooved, left median tooth than in *R. ninfasiensis* (Figure 4).

Retrotapes striatolamellata (Ihering, 1897)
Figures 33, 37–39, 42–47

Marcia striatolamellata Ihering, 1897:253, pl.7, fig.44, Ihering, 1907:305.

Marcia navidadis Philippi, Ortmann, 1902:141, pl.27, fig.12.

Marcia ortmanni Ihering, 1907:304

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Figures 29–31. *Retrotapes scutata* (Ihering). All figures 2×. Holotype MACN 429, Cañadón El Lobo, San Julián Formation, late Eocene. **29.** Left hinge, **30.** exterior and **31.** dorsal views of left valve. **Figure 32.** *Retrotapes fuegoensis*, new species 1×. Exterior view of left valve of holotype, PU 356–12, Cerro Castillo, Carmen Silva Formation, late Oligocene-early Miocene.

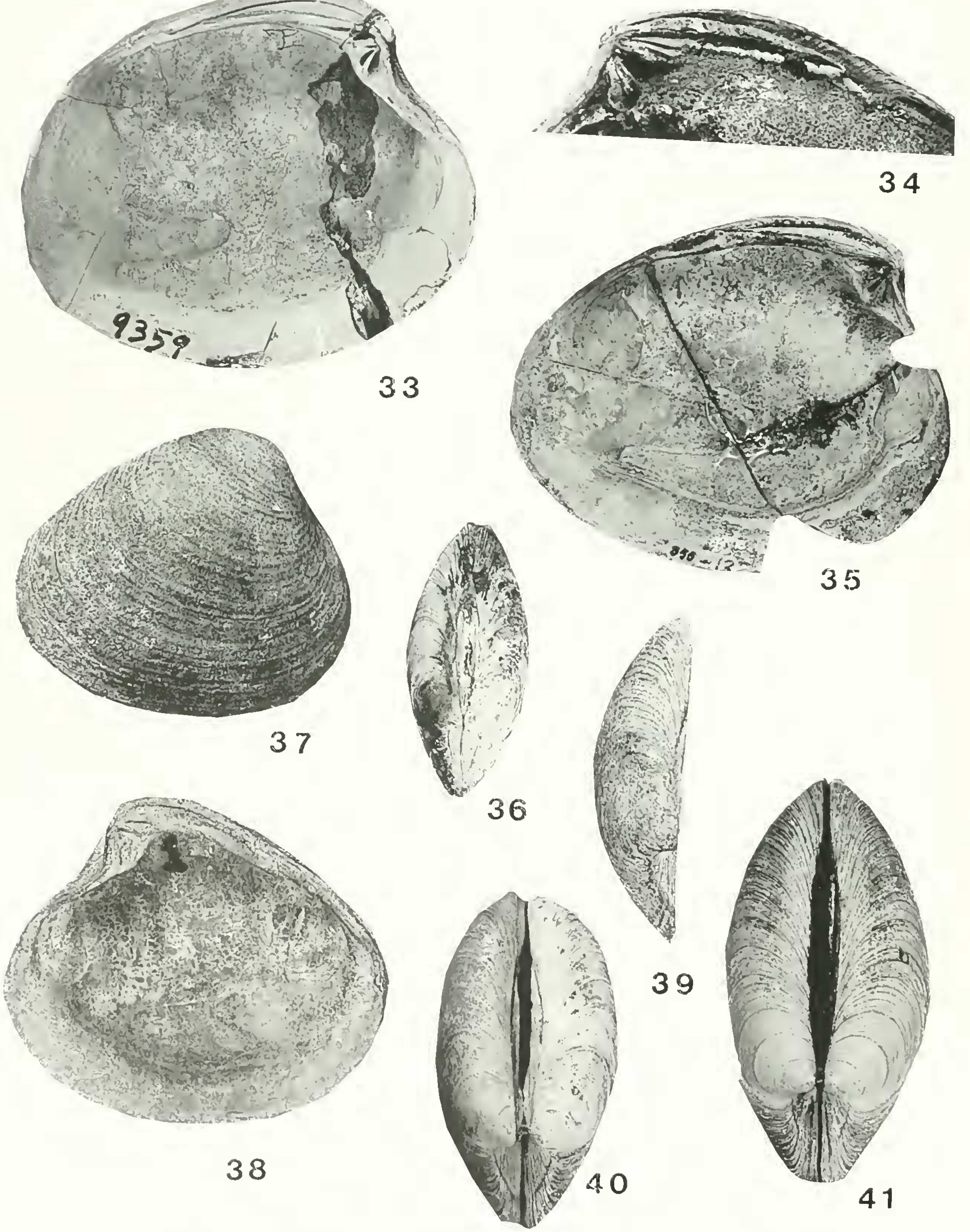


Figure 33. *Retrotapes striatolamellata* (Ihering) Interior view of left valve, CPBA 9359, Monte Entrada, Monte León Formation, late Oligocene (1×). **Figures 34–36.** *Retrotapes fuegoensis*, new species, Carmen Silva Formation, late Oligocene-early Miocene. **34.** Enlargement of right hinge, DNSG 16.500, Estancia La Federica (2×), **35.** Interior view of left valve of holotype PU 356-12, Cerro Castillo (1×). **36.** Dorsal view of an articulated paratype DNSG 16.501, Estancia La Federica (1×). **Figures 37–39.** *Retrotapes*

Diagnosis: Shell thick, ovate to subrectangular in outline, longer, more convex than *R. ninfasiensis*. Lunule strongly concave, not inclined toward opposite valve. Left anterior tooth arched (in most specimens), equal in height to median cardinal. Pallial sinus tongue-shaped, longer than in *R. ninfasiensis*.

Description: Shell thick, large, ovate to subrectangular, moderately convex, longer than high. Umbones small, at anterior quarter of length. Dorsal and anterior margins convex, ventral margin slightly convex, posterior margin slightly convex to subtruncated. Lunule broad, deeply concave, nearly vertical, not inclined toward opposite valve, marked by deep groove and distinctive ridge; longitudinal, median, lunular groove impressed. Escutcheon on left valve better defined than on right, consisting of wide, flat surface facing opposite valve, sculptured with very faint commarginal ridges. Escutcheon on right valve narrower than on left, heavily ornamented like remaining valve surface. Hinge with three narrow cardinal teeth; right valve with cardinal sloping backwards, lamellar anterior tooth, median cardinal narrowly and shallowly grooved, as high as or higher than anterior tooth. Posterior tooth broadly grooved, separated from nymph by ridge; anterior tooth of left hinge lamellar, arched, vertically or slightly inclined backwards, median tooth deeply grooved, broad, as high as, or higher than anterior tooth, narrow, straight or arched posterior cardinal tooth. Muscle adductor scars equal in size, shallowly impressed Pallial sinus deep, tongue-shaped. Commarginal sculpture of thin lamellar ridges, much more closely spaced near ventral margin. Interspaces smooth, except for growth lines.

Material examined: Holotype, MACN 437, right valve, Yegua Quemada, height 67.5 mm, length 79.3 mm; Paratypes, two left valves, Yegua Quemada, MACN 2639, height 65.0 mm, length 68.0 mm, and MACN 2640, height 65.0 mm, length 68.0 mm; two left and two right valves from Monte Entrada, CPBA 9.359, PU429, Las Cuevas, CPBA 9.391, and from Cerro Puntudo (Lago Cardiel) CIRGEO-PI 2.513. (Ihering, Ortmann, Medina and Camacho collections)

Stratigraphic and geographic distribution: Monte León Formation (late Oligocene), from the mouth of the Santa Cruz River to Yegua Quemada, and El Chacay Formation (late Eocene), Cerro Puntudo (Lago Cardiel).

Remarks: *Retrotapes striatolamellata* comes from outcrops of the Monte León Formation at Monte Entrada, Las Cuevas and Yegua Quemada (Figure 2). This species has also been recorded from exposures of the El Chacay Formation at Cerro Puntudo (Lago Cardiel) (Santa Cruz Province). The type material of *R. striatolamellata* had been collected by Carlos Ameghino at Yegua Quemada, but this fossiliferous locality has never been recognized by subsequent authors. Ortmann (1902) placed *R. striatolamellata* in synonymy with *R. navidadis* (Philippi, 1887). Ihering (1907) considered Ortmann's specimens to represent a new taxon that he named *Marcia ortmanni* Ihering, 1907. However, a re-analysis of Ortmann's material (1902, plate 27, figure 12) (Figure 47), reveals them to be young specimens of *R. striatolamellata*.

Material coming from Cerro Puntudo (Lago Cardiel) (Figures 37–39) is limited to a poorly preserved right valve with an eroded hinge. It is placed in *R. striatolamellata* because of the arrangement of teeth, shape and size of pallial sinus, characteristics of lunule, escutcheon and exterior commarginal ornamentation. The only difference between this specimen and those coming from the Monte León Formation is in the outline of the shell. While the Cerro Puntudo specimen has a narrowly convex posterior margin with an ovate-subtriangular outline, most representatives of *R. striatolamellata* from eastern Patagonia have shells with outlines ranging from subrectangular to ovate, with a broadly convex or truncated posterior margin (Figures 33, 42–46).

Retrotapes navidadis (Philippi, 1887) is distinguished from *R. striatolamellata* in having a thinner and smaller shell with a straight dorsal margin, narrower and less concave lunule, shorter and narrower teeth and more widely spaced and homogeneously distributed commarginal ridges than in *R. striatolamellata*. *Retrotapes lenticularis* has a subcircular shell with a narrower and less concave lunule, lower and more shallowly grooved teeth than in *R. striatolamellata*, a vertical right anterior tooth, right and left posterior teeth that slope backwards, and a pallial sinus with an acute apex and concave ventral margin. *Retrotapes striatolamellata* may be easily separated from *R. antarctica* (Sharman & Newton, 1894), which has a trigonally suboval shell, slightly concave lunule, narrower teeth, a right anterior tooth that is inclined forward, and a shorter and triangular pallial sinus than *R. striatolamellata*.

Retrotapes scutata (Ihering, 1907)
Figures 29–31

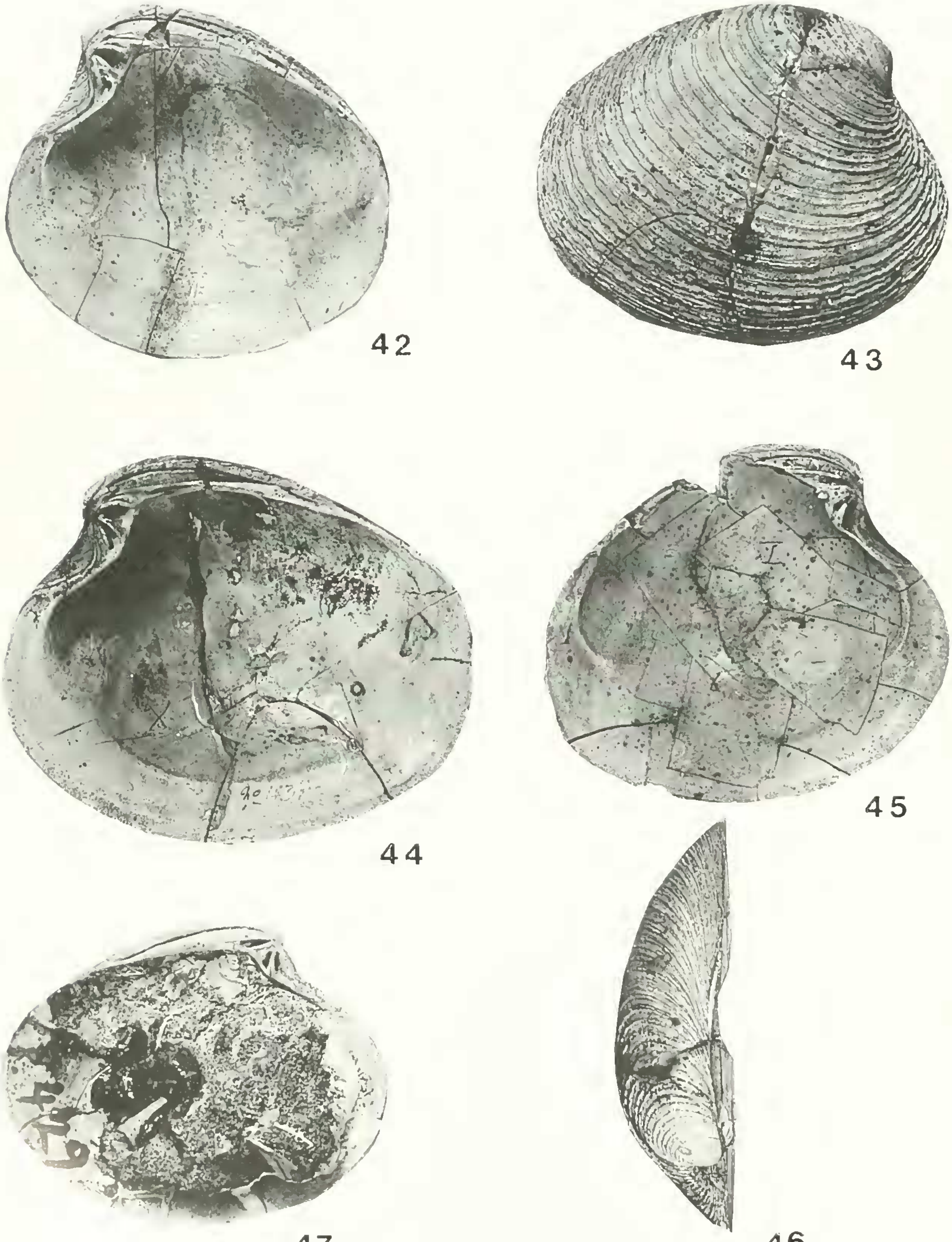
Marcia scutata Ihering, 1907:303, pl.11, fig.76.

Diagnosis: Shell, elongate-oval in outline, anterior margin convex. Lunule narrow, slightly concave.

Description: Shell of medium size, elongate-oval in outline, weakly convex, longer than high. Dorsal margin

←

striatolamellata (Ihering), CIRGEO-PI 2513 Cerro Puntudo, El Chacay Formation, late Eocene. All figures 1×. **37.** Exterior, **38.** interior and **39.** dorsal views of right valve. **Figure 40.** *Retrotapes ninfasiensis*, new species, CPBA 15.087, Punta Norte, Puerto Madryn Formation, middle Miocene. Dorsal view of articulated specimen (1×). **Figure 41.** *Retrotapes exalbida* (Chemnitz), MACN 21.172, San Matías Gulf, Argentina, Recent. Dorsal view of an articulated specimen (1×).



Figures 42–47. *Retrotapes striatolamellata* (Ihering). Monte León Formation, late Oligocene. **42.** Interior view of right valve of paratype, MACN 2639, Yegua Quemada (1×). **43.** Exterior, **44.** interior, and **46.** dorsal views of the holotype, MACN 437, Yegua Quemada (1×). **45.** Interior view of left valve of paratype, MACN 2640, Yegua Quemada (1×). **47.** P-429, Monte Entrada, interior view of left valve of juvenile specimen illustrated by Ortmann (1902:27, fig.12) (2×).

steeply sloping donwards, rounding to posterior margin; anterior margin narrowly convex. Lunule narrow, shallowly concave, not inclined toward opposite valve. Escutcheon on left valve strongly sloping toward right valve. Left hinge narrow, with lamellar anterior cardinal tooth sloping backwards, median tooth deeply grooved, posterior tooth lamellar, horizontal, slightly curved. Exterior with lamellar commarginal ridges. Interior unknown.

Material examined: Holotype, MACN 429, left valve, Cañadón El Lobo, height 32,0 mm, length 38,0 mm. (Ihering Collection).

Stratigraphic and geographic distribution: San Julián Formation (late Eocene) from Cañadón El Lobo (Santa Cruz Province).

Remarks: *Retrotapes scutata* is known only from the holotype, a left valve whose interior is unknown and the hinge partially covered with marl. The elongate-oval outline, narrow, slightly impressed lunule and thin cardinal teeth, separate this species from *R. striatolamellata* and *R. ninfasiensis*. *Retrotapes scutata* and *R. newtoni* (Wilckens, 1911: plate 1, figure 16; Zinsmeister, 1984: figure 9 I, H, K, Eocene-early Oligocene? La Meseta Formation, Antarctica), share similar features including outline, ornamentation, characters of the lunule, and arrangement of cardinal teeth. These similarities suggest that these species are very closely related. A more thorough comparision between *R. scutata* and R. *newtoni* is not possible until more material of *R. scutata* is collected.

Retrotapes fuegoensis new species
Figure 32, 34–36

Eurhomalea ? cf *fuenzalidai*, Malumián *et al.*, 1978:278, pl.3, fig.4, not *Venus fuenzalidae* Philippi, 1887.

Diagnosis: Shell elongate-oval in outline, anterior margin subtruncated, posterior margin convex. Cardinal teeth lower, narrower than in both *R. striatolamellata* and *R. ninfasiensis*, right anterior tooth straight, vertical, right median tooth shallowly grooved. Lunule very narrow, shallowly concave. Pallial sinus tongue-shaped, much deeper than in *R. striatolamellata*.

Description: Shell large to medium sized, weakly convex, elongate-oval, longer than high. Umbones at 1/9 of dorsal length. Dorsal margin slightly convex, rounding to convex posterior margin; anterior margin subtruncated. Lunule very narrow, shallowly depressed to nearly flat, not inclined toward opposite valve, broader in left valve than in right valve, with slightly marked median radial sulcus, bounded by moderately deep lunular groove. Escutcheon narrow, slightly broader in left valve than in right valve, with strongly sculptured commarginal ridges on both valves. Hinge with anterior tooth vertical, median and posterior teeth inclined backward. Left hinge with strong, high anterior tooth, median cardinal rectangular, bifid, with both parts equal in size, as high as anterior tooth, posterior cardinal lamellar, curved. Right valve with thin anterior tooth, narrow grooved median tooth, thin, deeply grooved posterior tooth. Exterior with strong, rounded, commarginal ridges, more crowded toward ventral margin.

Material examined: Holotype, PU 355–12, left valve, Cerro Castillo height 62.0 mm, length 73.0 mm (Zinsmeister Collection); Paratypes, articulated specimen, DNSG 16.501, height 48.3 mm, length 58.8 mm, right valve DNSG 16.502, height 32.8 mm, length 27.0 mm; six articulated specimens, one left valve, two right (Malumián Collection), and one fragment with left hinge from Estancia La Federica and Cerro Castillo PU 357–16, PU 355–13, DNSG 16.500, 16.503–16.509 (Zinsmeister and Malumián Collections).

Stratigraphic and geographic range: Carmen Silva Formation (late Oligocene-early Miocene), Cerro Castillo and Estancia La Federica, Isla Grande de Tierra del Fuego.

Remarks: *Retrotapes fuegoensis* comes from the uppermost conglomerated beds of the Carmen Silva Formation's exposures at the quarrel of Estancia La Federica and at Cerro Castillo, where it is associated with a highly diverse and well preserved molluscan fauna previously studied by Malumián, Camacho and Gorroño (1978). The outline of *R. fuegoensis* is the most distinctive character that readily distinguishes this species from its congeners. Based on examined material, the Chilean Neogene species *Venus colchaguensis* Philippi, 1887 (=*V. fuenzalidai* Philippi, 1887) may be also included in the genus *Retrotapes*. It differs from *R. fuegoensis* in having an acuminate anterior margin, a poorly defined escutcheon, and commarginal sculpture that consists of widely and uniformly spaced lamellae. *Retrotapes ninfasiensis* may be distinguished from *R. fuegoensis* by its ovate to subrectangular, posteriorly truncated shell, a more concave and broader lunule facing the opposite valve, much larger cardinal teeth, median and anterior teeth that strongly slope backward, and a triangular and shorter pallial sinus than in *R. fuegoensis*. *Retrotapes striatolamellata* differs from *R. fuegoensis* in having a shell that is ovate, more convex, and more acuminate anteriorly, with a lunule that is more concave and broader, and teeth that are larger than in *R.fuegoensis*. *Retrotapes scutata* has a more elongate and ovate shell, with a more concave lunule than *R. fuegoensis*. *Retrotapes antarctica* is characterized by a trigonally suboval shell with umbones placed more posteriorly, an anterior margin that is not truncated, and a smaller triangular pallial sinus than that of *R. fuegoensis*, as well as a right anterior tooth that inclines slightly forward. *Retrotapes newtoni* has an ovate, smaller shell that is not subtruncated anteriorly. It also has a more concave lunule, thinner teeth and a shorter pallial sinus than *R. fuegoensis*. The Recent species *R. exalbida* and *R. lenticularis* have subrectangular and subcircular outlines respectively, deeper, concave lunules and shorter pallial sinuses than *R. fuegoensis*.

DISCUSSION

Fleming (1963) proposed that Neoaustral faunal elements originated in the low latitudes of the Pacific margins during the late Tertiary. However, Zinsmeister (1982,1984) pointed out that at least some components of this fauna would have originated during the early Tertiary in high latitudes of circumpolar regions, and subsequently radiated northward. Antarctic Eocene records of *Aulacomya* Mörch, 1853, *Gaimardia* Gould, 1852, *Gomphina* Mörch, 1853 and *Eurhomalea* Cossmann,1920, led Zinsmeister to consider these to be Neoaustral taxa that originated in the higher austral latitudes much earlier than Fleming suspected.

The transfer to *Retrotapes* of Antarctic species previously assigned to *Eurhomalea* (Zinsmeister, 1984; Stilwell & Zinsmeister, 1992) limits *Eurhomalea* to strata younger than the Pleistocene. *Eurhomalea* most likely originated in Chile during the Pleistocene, later reached the Peruvian littoral fauna, and is now restricted to the eastern Pacific coast. *Retrotapes*, however, is a Neoaustral genus that appeared in Patagonian and Antarctic regions during the early Tertiary.

According to present data, *Retrotapes* first appeared in the southwestern Atlantic Ocean by the Eocene. It occurs in the late Eocene San Julián Formation and the El Chacay Formation of Patagonia, as well as in the Antarctic La Meseta Formation of late Eocene-Oligocene? age. By the early Miocene, *Retrotapes* expanded northward into the middle Chilean region, reached northern Patagonia by the middle Miocene, and attained its northermost distribution (*R. lenticularis* and *R. exalbida*) during the Holocene (Figure 1). Fleming (1963) and Zinsmeister (1982, 1984) agreed that cool seawater temperatures were related to the presence of Neoaustral taxa. Zinsmeister (1982) stated that the development of Neoaustral faunal elements in the early Tertiary of Antarctica reflects the cool water temperatures that existed in that region during the late Eocene. He also considered the absence of Neoaustral genera in earlier Tertiary deposits of South America to indicate the lack of suitable climatic conditions for the development of this fauna.

The present study records a new, Tertiary and Holocene, Neoaustral genus in southern South America, and suggests that it has adapted to a wide range of water temperatures that fluctuated from cool-temperate to warm. Estimates of Antarctic late Eocene paleotemperatures range widely among authors. Kennett (1977) calculated Eocene sea-surface temperatures around Antarctica to have been 9–12°C higher than today, while Feldmann and Zinsmeister (1984) indicated that cool temperate conditions occurred in the area. More recently, Stilwell and Zinsmeister (1992) indicated that, although cool to warm conditions may be inferred from marine invertebrate faunas, the molluscan fossils indicate warm-temperate conditions during the deposition of the La Meseta Formation.

Despite discrepant inferences of paleotemperatures, mollusks reveal that Antarctic conditions during the late Eocene were cooler than those in southern Patagonia during both the Eocene and Oligocene, as well as those recorded during the middle Miocene of northern Patagonia. Del Río (1990, 1994 a,b), inferred warm temperatures for northern Patagonia during the middle Miocene based on the presence of tropical and subtropical genera as *Amusium*, *Flabellipecten*, *Chionopsis*, *Antinioche*, *Hexacorbula*, *Miltha*, *Egeta*, *Arca*, *Dosinia s.str.* and *Lucinisca*. According to del Río (1990, 1994 a,b), middle Miocene temperatures in northern Patagonia would have been similar to those of the tropical Panamic Molluscan Province and the warmest regions of the Gulf and Caribbean Molluscan Provinces. Along the Patagonian litoral, temperatures decreased steadily, with cooler conditions similar to those occurring today having been established by the end of middle Miocene times. Almost 70% of the middle Miocene genera became extinct, including all of the above mentioned tropical and subtropical genera. *Retrotapes*, however, continued to live in this region adapting to the new climatic conditions. Its present distribution is restricted to the warm temperate Argentinian Province and to the cool-temperate Magellanic Province.

Recent advances in our knowledge of Antarctic and Patagonian molluskan assemblages (Zinsmeister & Camacho, 1980; Zinsmeister, 1976,1981,1984; Camacho & Zinmeister, 1986; Griffin, 1991; Stilwell & Zinmeister, 1992) show that the ocurrence of *Retrotapes* in Patagonia and Antarctica, along with several other genera and subgenera, including *Periploma (Aelga)* Slodkewitsch, 1935, *Pteromyrtea* Finlay, 1927, *Lahillia* Cossmann, 1899, *Crassatella* Lamarck, 1799, *Aulacomya* Mörch, 1853, the gastropods *Struthiolarella* Steinmann and Wilckens, 1908 and *Eoscaphella* Stilwell and Zinsmeister, 1992, as well as nuculoids, arcoids (del Río & Camacho, 1997) and veneroids that are presently being studied, reinforces the similarities in paleoclimates of southern South America and the Antarctic continent during the Paleogene, even after the final break-up of the Weddellian Province.

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